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ABOUT RESPIRATION RHYTHMS OF INSECTS

Very little attention has so far been paid to the respiration rhythms of insects in literature. Most papers deal with the cyclic release of carbon dioxide. This phenomenon is described in predator bugs, beetle larvae (Куузик, Когерман, 1978) and adult beetles (Punt, 1950; Punt et al., 1957; Куузик, 1976), wintering butterfly caterpillars and imagos (Punt, 1950), adult grasshoppers and cockroaches (Buck, 1962). Diapausing butterfly pupae have been studied in greater detail (Punt, 1950; Schneiderman, Williams, 1953; 1955; Buck, Keister, 1955; Куузик, 1977; Метспалу, Сейн, 1985).

The cyclic CO_2 release is accompanied by a low level of metabolism. All the authors note that the frequency of cycles changes during metamorphosis.

Data about other respiration rhythms are practically lacking. It is of interest to note that active respiration micromovements were found only in 60% of the individuals of cecropia pupae (Brockway, Schneiderman, 1967).

The study of respiration intensity alone may give quite a lot of information on the physiological state of insects. It is clear that measuring respiration rhythms and the intensity of respiration together enables to get a more exact picture about the physiological state.

No generalizing treatments of respiration rhythms are available. The cyclic CO_2 release has been investigated only as an interesting physiological phenomenon. The reason of this situation lies in methodological difficulties. The equipment used for respiration measurements at present is not fit for such experiments. Besides, the respective apparatus is not produced commercially.

The purpose of the present study is to determine respiration rhythms and to give their general review. Several causes for the occurrence of various types of rhythms are discussed.

Material and methods

An improved electrolytical respirometer was used (Устройство для . . . , 1980) which enables to register the respiration level and rhythms simultaneously. Experiments were carried out in summer from 1985 to 1989.

Insects for experiments were caught from nature a day before measurements. Up to the beginning of the experiment insects were not fed. Bred cockroaches (*Blattella germanica*) and wax moths (*Galleria mellonella*) were studied additionally. Species for experiments were selected according to the principle that mainly larger orders would be represented. The number of beetles used was largest since due to their hard cover the form of respiration movements changes very little, and so methodological errors were supposed to be the smallest. The temperature was mainly 20 °C and 25 °C, in some cases 15°C, 30 °C and 35 °C. When the individuals were used on two consecutive days, they were kept in Petri dishes without food in the presence of a wet piece of filter paper. When an experiment lasted longer, adults were fed according to their diet in nature.

The respiration rate, frequency and amplitude of the rhythm, the duration of the rhythm unit and the pause between the rhythm units were measured on the respirogram. However, the direct value of the amplitude corresponding to the extent of respiration movements or the amount of the gas released could not be measured because of the lack of linear correlation between the registration current and the pressure change caused by the respiration movements of the insect in the working chamber of the respirometer. That is why the change of the respiration current in milliampers was taken as a dimension of amplitude.

Experiments where any measured value differed essentially from the general complex were not taken into account in computing the mean values.

Results

1. Types of respiration rhythms

Altogether 99 measurements were carried out. On the basis of the experiments it is possible to distinguish between 6 types of rhythms whose numerical data are presented in Table 1.

Table 1

Types of respiration rhythms [1]

Type of rhythm	Number of measurements	Mean				
		Respiration level, $mm^3O_2/mg/h$ (min-max)	Frequency[2], 1/h	Amplitude, mA	Duration of rhythm unit, s	Duration of pause,[3] s
1. Microrhythm	27	2.37 (0.53—4.80)	1698	0.45	1.65	1.69
2. Micromacrorhythm	7	1.05 (0.60—2.00)				
a) microrhythm	4		1248	0.065	1.94	3.73
b) macrorhythm			10.9	0.152	720	1896
3. Microrhythm + micromacrorhythm	2	0.86 (0.60—1.12)				
a) microrhythm			276	0.11	2.0	12.0
b) macrorhythm			0.8	0.210	600	3675
4. Microrhythm + CO_2 macrorhythm	6	2.04 (1.55—2.50)				
a) microrhythm			2322	0.134	0.87	1.04
b) CO_2 macrorhythm			75.2	0.348	14.4	43.2
5. CO_2 macrorhythm	15	1.22 (0.33—3.60)	49.8	0.158	24.6	83.4
a) flutter	2		1578	0.004	1.9	0.35
6. Arhythmicity	42	2.76 (0.55—7.50)	—	—	—	—

[1] Rhythm unit in microrhythms is inspiration + expiration; in micromacrorhythms a group of microrhythms; in CO_2 macrorhythms a CO_2 burst.
[2] Frequency is the number of rhythm units per hour.
[3] Pause is the time between two rhythm units.

In the first type gas exchange takes place continuously together with active respiration movements. This will be called the type of active respiration microrhythms. A typical respirogram is shown in Fig. 1. An active decrease of the abdomen, or expiration, takes place first, followed by inspiration. Microrhythms were found in the following species: *O. Blattoptera — Blattella germanica; O. Coleoptera — Adoxus obscurus, Chlorophanus viridis, Cicindela hybrida, Coccinella septempunctata, Phyllopertha horticola, Pterostichus coerulescens; O. Diptera — Helophilus trivittatus, Lucilia caesar; O. Hemiptera — Carpocoris purpureipennis; O. Hymenoptera — Tenthredinidae* gen. sp.. All were adults.

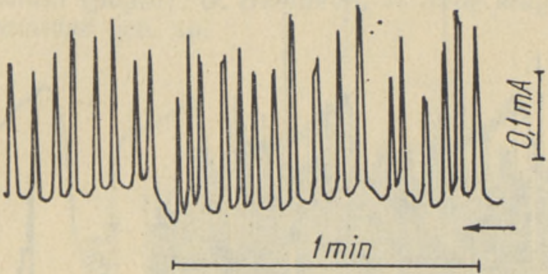


Fig. 1. Microrhythms, *Pterostichus coerulescens*, $t=20\,°C$, respiration level 1.30 mm^3 O_2/mg/h.

In the second type respiration movements are assembled into groups between which the movements are absent or irregular and sparse. This will be called the type of micromacrorhythms. A typical respirogram is presented in Fig. 2. Micromacrorhythms are characterized also by the values of microrhythms in groups. Micromacrorhythms were found in the species: *O. Blattoptera — Blattella germanica; O. Hymenoptera — Andrena denticulata, Tenthredinidae* gen. sp., *O. Lepidoptera — Galleria mellonella* (pupae). It is interesting to note that micromacrorhythms did not occur in any beetle.

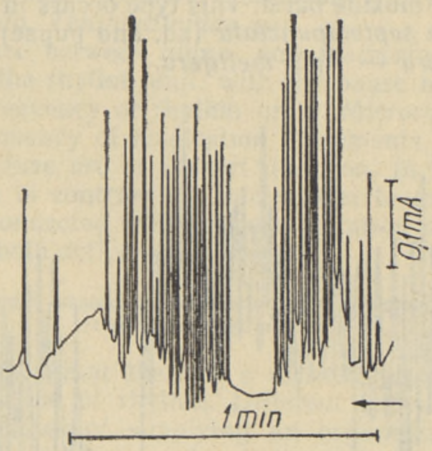


Fig. 2. Micromacrorhythms, *Tenthredinidae* gen. sp., $t=25\,°C$, respiration level 0.70 mm^3 O_2/mg/h.

The third type is characterized by joint occurrence of microrhythms and micromacrorhythms. The corresponding respirogram is shown in Fig. 3 *A*. This picture has some similarity with CO_2 macrorhythms (see below), with a typical carbon dioxide burst being noticeable. Nevertheless, there is reason to consider this type as belonging to microrhythms because its frequency is considerably higher than in macrorhythms. Active respiration movements are clearly seen, too (Fig. 3, *B*). It is possible, however, that the application of additional investigation methods and improved knowledge will change the interpretation of this type. This rhythm type was met only in *Galleria mellonella* pupae.

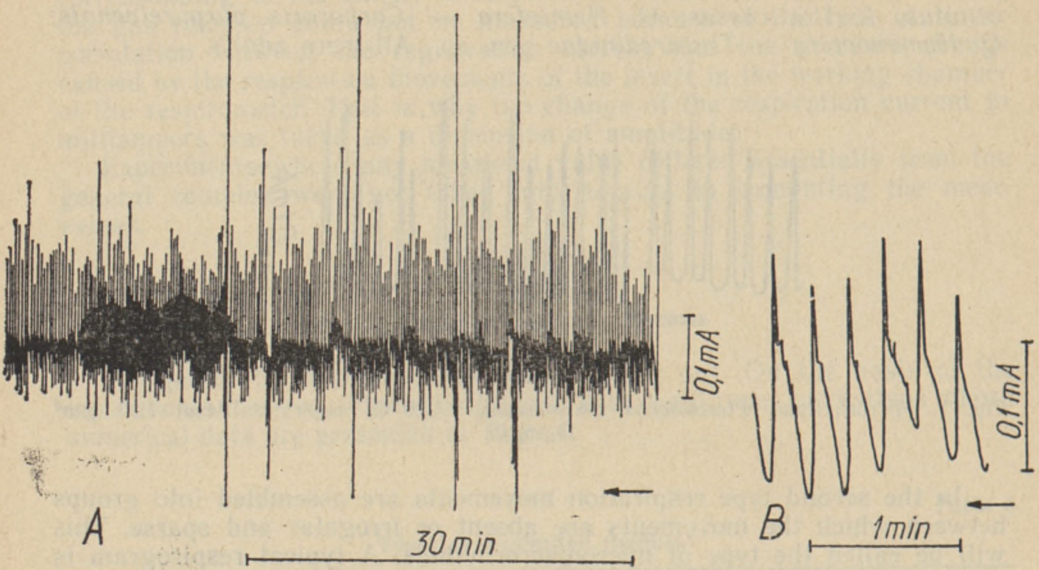


Fig. 3. Microrhythms with micromacrorhythms, *Galleria mellonella*. *A* — on the left a group of microrhythms can be seen. *B* — magnified microrhythms, $t=28$ °C, respiration level 0.60 mm³ O_2/mg/h.

In the fourth type microrhythms are accompanied by carbon dioxide bursts (Fig. 4). It is interesting that microrhythms do not disappear at the time of a carbon dioxide burst. This type occurs in the species: *O. Coleoptera — Coccinella septempunctata* (ad. and pupae), *Phyllopertha horticola; O. Hymenoptera — Apis mellifera.*

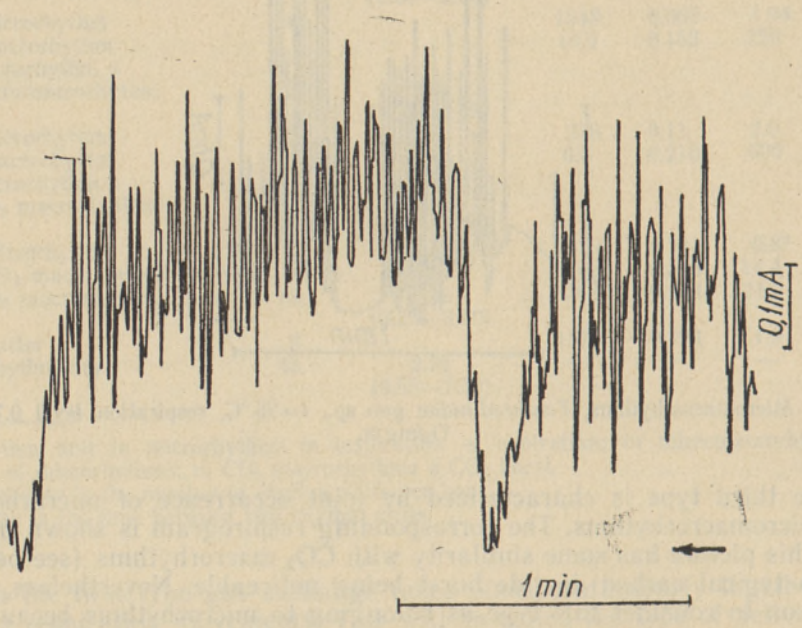


Fig. 4. Microrhythms with CO_2 macrorhythms, *Coccinella septempunctata pupae*, $t=25$ °C, respiration level 1.96 mm³ O_2/mg/h.

The fifth type is that of pure carbon dioxide macrorhythms. In literature this phenomenon is called cyclic carbon dioxide release. A characteristic respirogram is presented in Fig. 5. Between CO_2 bursts it is also possible to observe small respiration movements to be called the flutter. Carbon dioxide macrorhythms were met with in the species: *O. Blattoptera — Blattella germanica; O. Coleoptera — Cicindela hybrida, Dermestes lardarius* (ad. and pupae), *Strangalia melanura, Coccinella septempunctata* (pupae)*; O. Hemiptera — Aelia klugi; O. Hymenoptera — Tenthredinidae* gen. sp.

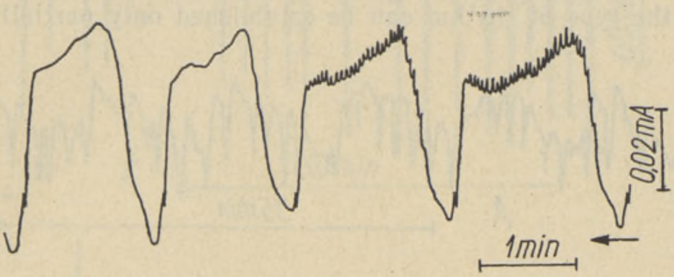


Fig. 5. Carbon dioxide macrorhythms, *Dermestes lardarius*, $t=20\,°C$, respiration level 0.45 mm^3 O_2/mg/h.

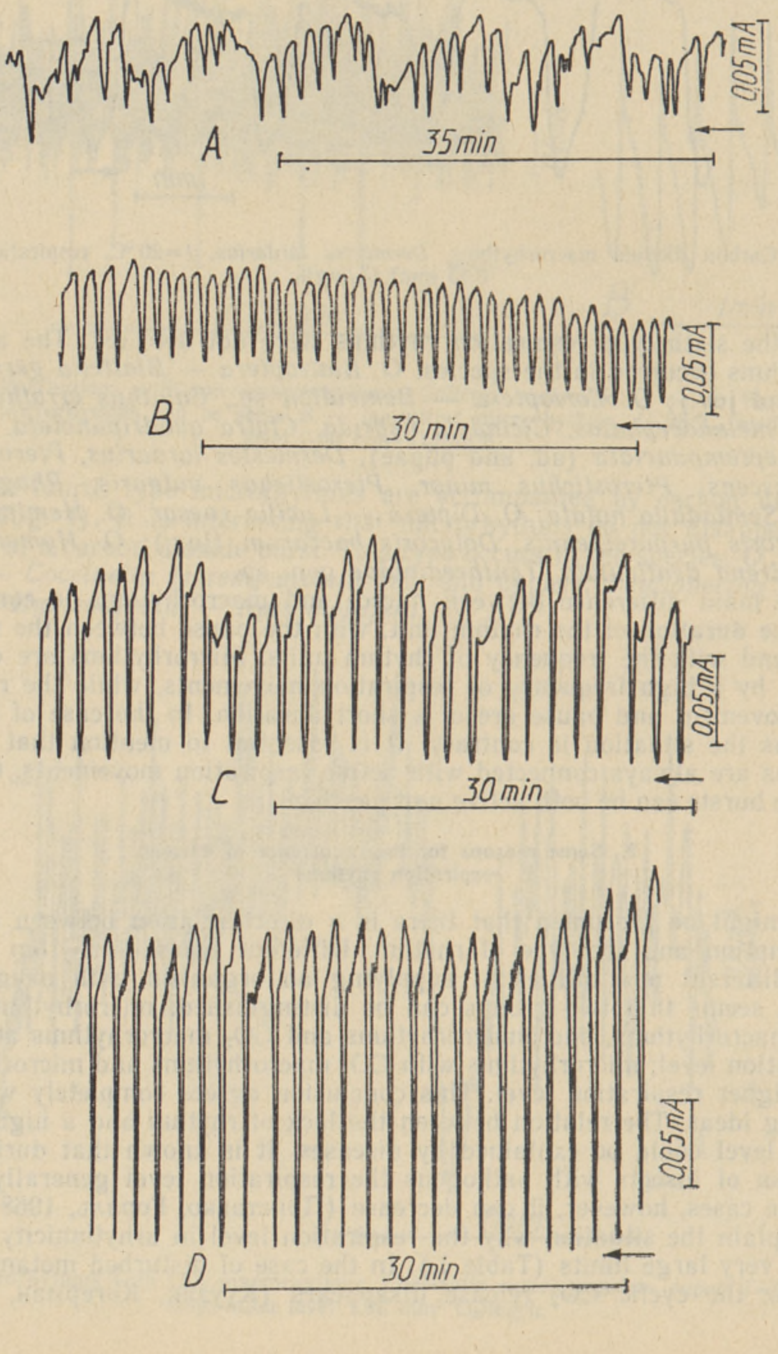
In the sixth type respiration rhythms were not detected. The absence of rhythms occurred in the species: *O. Blattoptera — Blattella germanica* (ad. and juv.); *O. Coleoptera — Bembidion* sp., *Calathus errathus, Calathus melanocephalus, Cicindela hybrida, Clytra quadripunctata, Coccinella septempunctata* (ad. and pupae), *Dermestes lardarius, Pterostichus coerulescens, Pterostichus minor, Pterostichus vulgaris, Rhagonycha fulva, Semiadalia notata; O. Diptera — Lucilia caesar; O. Hemiptera — Carpocoris purpureipennis, Dolycoris baccarum* (juv.); *O. Hymenoptera — Andrena denticulata, Tenthredinidae* gen. sp.

The main difference between micro- and macrorhythms is connected with the duration of the rhythm unit, with the pause between the rhythm units and with the frequency of rhythm units. Microrhythms are characterized by a high frequency of respiration movements, while the respiration movement and pause are of a short duration. In the case of macrorhythms the situation is contrary. It is essential to mention that microrhythms are always connected with active respiration movements. Carbon dioxide bursts can be both active and passive.

2. Some reasons for the occurrence of various respiration rhythms

It might be presumed that there is a direct relation between oxygen consumption and the type of rhythm. Different types of rhythm should have different possibilities of supplying an organism with oxygen. At first it seems that two groups can be distinguished: microrhythms with micromacrorhythms, micromacrorhythms and CO_2 macrorhythms at a low respiration level; microrhythms with CO_2 macrorhythms and microrhythms at a higher respiration level. This conclusion agrees completely with the existing ideas. The relation between the lack of rhythm and a high respiration level could be explained by diseases. It is known that during the infection of insects with pathogens the respiration level generally rises, in some cases, however, it can decrease (Приставко, Гораль, 1968). This can explain the situation why the respiration level in arhythmicity varies within very large limits (Table 1.). In the case of disturbed metamorphosis, too, the cyclic CO_2 release disappears (Куузик, Когерман, 1978).

However, in this case about 45% of individuals in nature should have physiological deflections, which is hardly possible. It is evident that some other factors must also determine the different occurrence of CO_2 macro-rhythms and micromacrorhythms, because in these rhythm types the respiration level is practically the same. Hence, it is possible to draw only one conclusion, namely, that there is no direct connection between the oxygen consumption level and the type of rhythm. There undoubtedly exists a certain dependence while the role of other influential factors should not be neglected. Thus, based on the mean values of the respiration rate in several types of rhythm the relation between the respiration level and the type of rhythm can be established only partially.



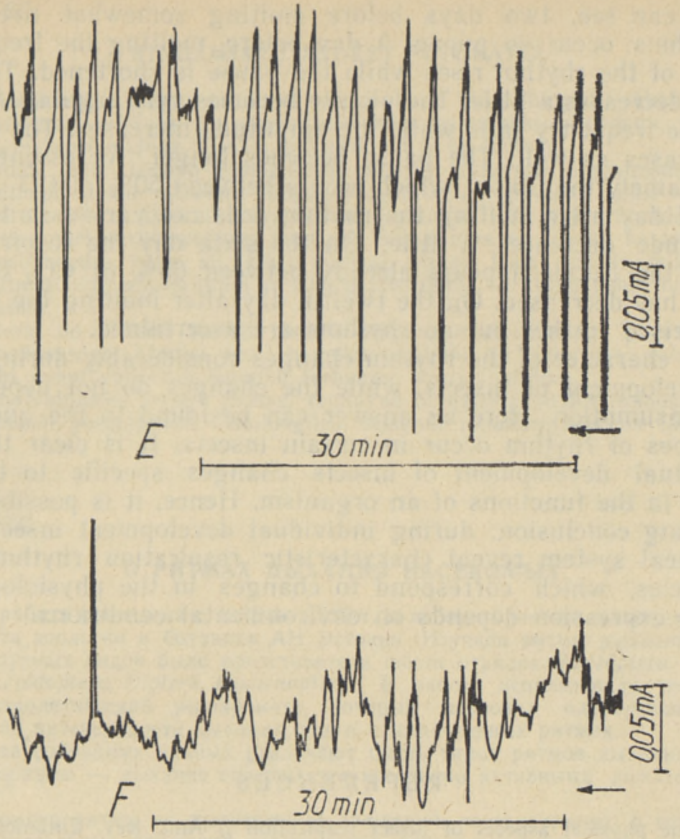


Fig. 6. Life-time changes in rhythms, *Dermestes lardarius*. *A* — 2 days before adult molting; *B* — 1 day before adult molting; *C* — 1 day after adult molting; *D* — 2 days after molting; *E* — 6 days after molting; *F* — 12 days after molting.

The situation becomes clearer when we make long-term observations of rhythms on one individual insect. Such an experiment was carried out with *Dermestes lardarius*. The experiment began with pupae two days before adult molting. Measurements were taken on four consecutive days and on the sixth and twelfth day after molting. During this time distinct changes took place in respiration rhythms. Respirograms are presented in Fig. 6. Numerical data are in Table 2.

Table 2

Life-time changes of rhythm (*Dermestes lardarius*) at 20 °C

Date	Oxygen consumption, mm^3 O_2/mg/h	Frequency, 1/h	Amplitude, mA	Duration of CO_2 burst, min	Duration of pause, min
			Pupa		
06. 09. 88	0.41	44	0.03	0.5	0.9
07. 09. 88	0.33	54	0.042	0.5	0.75
			Imago		
08. 09. 88	0.5	34	0.092	0.43	1.5
09. 09. 88	0.45	36	0.06	0.5	1.4
13. 09. 88	0.72	32	0.044	0.5	1.4
22. 09. 88	1.1	—	—	—	—

As we can see, two days before molting somewhat irregular CO_2 macrorhythms occur in pupae. A day before molting the frequency and amplitude of the rhythm rises while the pause is shortened. The respiration level decreases a little. The picture becomes very regular. A day after molting the frequency falls while the amplitude increases. The respiration level increases as well. The pause becomes longer. An essential change appears, namely the flutter, which occurs between 50% of CO_2 bursts. On the second day after molting the rhythm does not vary essentially while the amplitude decreases a little. On the sixth day the respiration level has risen, the flutter appears already between 65% of CO_2 bursts. The amplitude has decreased. On the twelfth day after molting the respiration level has risen further but no rhythms are ascertained.

So, the character of the rhythm changes considerably during the individual development of insects, while the changes do not depend on the oxygen consumption. Here an answer can be found to the question why certain types of rhythm occur in certain insects. It is clear that during the individual development of insects changes specific to the species take place in the functions of an organism. Hence, it is possible to make the following conclusion: during individual development insects with an open tracheal system reveal characteristic respiration rhythms, specific to the species, which correspond to changes in the physiological state and whose expression depends on environmental conditions.

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HINGAMISRÜTMIDEST PUTUKATEL

Avatud trahheesüsteemiga putukatel esineb kuut tüüpi hingamisrütme: 1) mikrorütmid, 2) mikromakrorütmid, 3) mikrorütmid koos mikromakrorütmidega, 4) mikrorütmid koos CO_2 makrorütmidega, 5) CO_2 makrorütmid ja 6) arütmia.

Mikrorütmide puhul toimub gaasivahetus pidevalt aktiivsete hingamisliigutuste abil. Mikromakrorütmide puhul esinevad hingamisliigutused gruppidena, mille vahel hingamisliigutusi ei ole või on üksikud korrapäratud liigutused. CO_2 makrorütmide puhul tuleb hingamises ette suuri süsihappegaasi purskeid. See nähtus on tuntud ka tsüklilise süsihappegaasi vabanemise nime all. Ühel putukal võivad koos esineda mikrorütmid ja mikromakrorütmid ning mikrorütmid ja CO_2 makrorütmid. Arütmia puhul hingamisrütme ei ole täheldatud.

Makrorütmid on üldiselt seotud madala hingamisintensiivsusega ja arütmia kõrge hingamisintensiivsusega. Kindlat seost hapniku tarbimise ja rütmitüübi vahel pole, sest iga rütmitüübi puhul varieerub hapniku tarbimine suurtes piirides.

Putuka individuaalse arengu jooksul toimuvad hingamisrütmides iseloomulikud muutused, mis ilmselt peegeldavad füsioloogilise seisundi muutumist ja on liigispetsiifilise iseloomuga.

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О РИТМАХ ДЫХАНИЯ НАСЕКОМЫХ

Данная работа проведена с 1985 по 1989 г. в лаборатории энтомологии и нематологии Института зоологии и ботаники АН Эстонии. Изучали ритмы дыхания насекомых. Среди исследуемых видов были представители шести отрядов: *Blattoptera, Hemiptera, Coleoptera, Lepidoptera, Diptera, Hymenoptera.* В работе использовали усовершенствованный электролитический респирометр, который позволил одновременно получить данные как об интенсивности дыхания, так и о дыхательных ритмах.

На основе собранных данных различают шесть типов ритмов дыхания:

1) микроритмы — дыхание совершается постоянно активными дыхательными движениями,

2) микромакроритмы — дыхательные движения сосредоточены в группы, между которыми дыхательные движения отсутствуют или происходят редкие нерегулярные дыхательные движения,

3) микроритмы вместе с микромакроритмами,

4) микроритмы вместе с CO_2-макроритмами,

5) CO_2-макроритмы — при дыхании наблюдается выделение углекислого газа цикличными залпами,

6) аритмию — дыхательных ритмов не обнаружено.

Основное различие между микро- и макроритмами заключается в частоте ритмов. Для микроритмов характерны большая частота дыхательных движений, короткое дыхательное движение и пауза. Микроритмы характеризуются низкой частотой единицы ритма (группа микроритмов или залп выделения углекислого газа), относительно большой длительностью единиц ритма и продолжительностью паузы между единицами.

Прямой связи между интенсивностью дыхания и типами ритмов не обнаружено.

В течение индивидуального развития в дыхательных ритмах наблюдаются процессы, которые отражают изменения в физиологическом состоянии насекомого и носят видоспецифический характер.